

University of Groningen

## Functional aspects of incubation in the herring gull (*Larus argentatus* Pont.)

Drent, Rudolf Herman

**IMPORTANT NOTE:** You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

*Document Version*

Publisher's PDF, also known as Version of record

*Publication date:*

1967

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Drent, R. H. (1967). *Functional aspects of incubation in the herring gull (*Larus argentatus* Pont.)*. Martinus Nijhoff/Brill.

### Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

### Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

## SUMMARY

### I. INTRODUCTION

This paper is concerned with the problem of how the parent Herring Gull (*Larus argentatus*), in the natural situation, contributes to providing and maintaining the conditions optimal to the development of the embryo. The work was carried out on the Dutch Frisian island Schiermonnikoog, by combining observations and measurements in the gull colony with simple experiments on the heat production of the developing embryo in the nearby field laboratory. It is important to bear in mind that, besides the problems dealt with here, protection of the clutch from predators is also a vital function of incubation behaviour in the Herring Gull. On Schiermonnikoog some 20 % of all eggs laid were eliminated by predation, which was heaviest early in incubation. Of the fertile eggs remaining, 85 % hatched, *i.e.* in meeting the physical demands of incubation loss was limited to 15 %.

### II. THE RHYTHM OF INCUBATION

The parents, who share incubation duties equally, alternate in *parental shifts* of several hours' duration. The available observations support the idea that the length of the parental shift is determined by the absence of the off-duty bird, and that this, in turn, is dependent on the foraging rhythm. The parental shifts are composed of periods of uninterrupted incubation, the *sitting spells*, and intervening interruptions, or *breaks*, during which, for instance, the parent may rise briefly at the nest and re-arrange the eggs before resuming incubation, or be driven from the nest by some disturbance. Information on these components of incubation rhythm, as well as their combination to give *attentiveness* (expressed as the number of minutes per hour, or per cent of the time, that the eggs are kept covered) can be interpreted from registrations of temperature in the nest. By utilizing small temperature recorders mounted in dummy eggs of copper, a large statistical material was obtained, and has been analysed with respect to the following three factors. 1) Time of day. In the laying period and the first week after clutch completion the parents, especially those nesting away from other Herring Gulls, often abandon their eggs during the hours of darkness. This is a carry-over of the diurnal

habitat shift described by TINBERGEN for the pre-egg stage. Later, in steady incubation, the hours of darkness are characterized by long sitting spells. This is seen as an expression of the rhythm of sleep and wakefulness, without functional correlates as far as the embryo is concerned. 2) Day of incubation. In the course of incubation there is first a spectacular increase in the length of the sitting spell and decrease in the breaks, such that attentiveness climbs steeply, and this is followed by a steady rise in attentiveness until the eggs pip. At that point sitting spells decline and breaks lengthen, and especially once the first chick has hatched this brings about a drastic reduction in the amount of time spent incubating the remaining eggs. For this reason it is important that the eggs hatch with a reasonable degree of synchrony, and as has been argued by BEER, this may be one of the reasons why effective incubation from the first egg on has not been evolved in gulls. 3) Weather. Surprisingly, the incubation rhythm of the Herring Gull was found to be unaffected by fluctuations in air temperature, at least in the range normally occurring (5–30 °C). Rainfall, however, caused the birds to sit more steadfastly. Perhaps the most striking outcome of the investigation was the impressively high attentiveness: when not disturbed by man the Herring Gull keeps the eggs covered an average of 98 % of the time from the onset of steady incubation after clutch completion until hatching starts. As shown by temperature measurements (IV.6), this high degree of attentiveness results in a protection of the eggs from environmental extremes.

### III. EGG POSITION

Following the lead of LIND's work on the Black-tailed Godwit, the mechanical consequences of the parent's actions on the position of the eggs was studied by measuring the variations in egg position in the nest, and comparing this with the position assumed by the egg when placed in water. In both cases only the variation about the long axis of the egg was recorded. A consideration of the records for individual eggs shows that egg position in the nest is not random. The water dish measurements demonstrated that eggs of the Herring Gull show a weight asymmetry within a week of clutch completion. Furthermore, with a few exceptions, the mean position in the water dish was practically identical to mean position of the egg in the nest. These observations indicate that gravity plays the ultimate role in deciding the position of the egg during incubation. To test this supposition, the effect of the parent's actions on the position of the eggs was investigated by substituting a transparent nest-bowl for the nest and observing from beneath. The records so obtained

suggest that the egg-shifting behaviour and foot movements of the parent have a corrective influence on egg position, in the sense that eggs displaced from their preferred position will be returned to it, whilst those already in the preferred position will not be altered. Towards the end of incubation the embryo was found to lie in a fixed relation to the part of the egg lying uppermost in the nest, such that during hatching the first hole will be formed at the top of the egg, providing the egg is in the position dictated by gravity. A similar situation was shown to obtain in the Domestic Fowl, thus obviating the need to assume a corrective rotation of the embryo within the shell prior to pipping in order that the hole be made uppermost.

As is known from research on artificial incubation, frequent turning in early incubation has the important function of avoiding premature adhesion of the embryo to the shell. The same doubtless holds true for natural incubation. The effect of the frequent jostling of the egg by the parent, however, is to restrict the position of the egg more and more as incubation proceeds. It is suggested that this may be functionally important in 1) keeping the embryo in the warmest part of the egg, 2) assuring that the respiratory organ, the allantois, grows out over the upper surface of the egg, 3) possibly reducing the chance of malpositions occurring during the shifting of the embryo within the egg described in III.3 and finally 4) facilitating hatching by causing the hole to be made uppermost.

#### IV. HEAT EXCHANGE DURING INCUBATION

The eggs of birds require external heat in order for the embryo to complete development. In the Herring Gull this is achieved at the metabolic cost of the parent, heat being transmitted to the three eggs by the application of three temporarily bare and highly vascular areas of the ventral body surface, the brood-patches (IV.2).

Temperature conditions in the nest were investigated during undisturbed incubation with the aid of thermistors (IV.3). At the interface between the brood-patch and the upper egg surface a constant temperature prevailed from clutch completion through hatching, the mean being 39.5 °C. At the lower egg surface/nest floor interface the temperature rose sharply in the course of incubation, the gradient through the egg declining from 12° at clutch completion to about 4° towards hatching. Temperature between the eggs rose, within four days, from about 33° at clutch completion to a plateau, averaging 35.8°. The mean for all determinations from clutch completion through hatching was 35.5°. The increase in parental attentiveness is believed responsible for the rise in

nest air temperature, and also for the rise in internal egg temperature (as measured at the centre of the egg or at the inner air cell membrane) observed in the week following clutch completion. Due to its position near the upper egg surface, the embryo itself, however, is kept at a nearly constant temperature of  $37.6^{\circ}$  during the first ten days, at least during the time that the egg is covered by the parent. Hereafter the embryo experiences a slight rise in temperature, reaching  $39^{\circ}$  towards the close of incubation. This rise is brought about by the heat production of the embryo (IV.4).

The heat production of the developing embryo was determined by incubating eggs singly in small respiration chambers at the field laboratory, and measuring the amount of  $\text{CO}_2$  expired (IV.4). At  $38^{\circ}$  the embryo liberated a total of 57.9 kcal in the course of incubation. Assuming that this was produced by the combustion of fat, this amount would represent a depletion of the fat reserves of the fresh egg by 60 %. The remainder can be drawn upon by the gull chick in its first days of life. The intensity of metabolism of the embryo up to the point of hatching (expressed as cal/g wet weight/hour) lies below that typical for the basal rate of adult birds of like weight. Cooling trials, simulating periods of parental absence in cool weather, failed to reveal any compensatory heat production by the embryo, the eggs cooling steadily and the embryonic heat production falling as well until a new equilibrium had been reached. The newly-hatched chick, by contrast, reacts to a fall in air temperature by an increase in heat production and has therefore a limited capacity to regulate its body temperature during cooling.

During incubation the avian egg loses weight as a result of the evaporation of water. The heat lost by the egg through evaporation can therefore be computed from records of weight loss. For this reason Herring Gull eggs were weighed every other day in the field, and a constant decrement of weight loss ( .45 g/egg/day) was found to hold from the time that definitive nest air temperature was established up to the time at which lung ventilation of the embryo set in (IV.5). This decrement corresponds to an evaporative heat loss of about 12 cal/egg/hour. A compilation from the literature shows that weight loss of the egg during incubation is proportional to the surface area of the avian egg, such that evaporative heat loss will be relatively highest in small eggs.

Following the procedure of KENDEIGH, the heat requirement of incubation was computed for the Herring Gull on the basis of the temperature gradients measured in the nest, together with the weight, specific heat, and cooling constant of the egg (IV.6). The applicability of the

procedure was verified by experiments with an artificial brood-patch in the laboratory. Although the embryo is not capable of maintaining its temperature alone, the share of embryonic heat production in the total heat requirement reaches 75 % at the close of incubation. The parental share of the Herring Gull in the energy demand of incubation varies between about 8.5–14.5 kcal/bird/day, which amounts to 20 %–30 % of the net energy estimated to be available to the parent Herring Gull on the basis of data for the Domestic Fowl.

In the absence of the parent the embryo Herring Gull risks death by either chilling or overheating, in the study area the latter danger being far the most urgent. The sitting gull seals the nest contents off from the outside air as far as temperature is concerned, and by the tenacious pattern of incubation (98 % of the time) effectively protects the clutch from both extremes. The Herring Gull thus achieves regulation of egg temperature by covering the clutch continuously, and the problem faced by the parent is the regulation of its own body temperature. In response to intense radiation, for instance, postural changes (drooping the wings, ruffling the plumage, or even standing at the nest) combined with evaporative cooling (panting) enable the parent to remain at the nest.